Potential effects of climatic warming on the distribution of Collembola along an altitudinal transect in Lamington National Park, Queensland, Australia

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ABSTRACT

Collembola were collected from pitfall traps at each of five altitudes, 300, 500, 700, 900 and 1100 m above sea level (a.s.l.) in Lamington National Park, Queensland. All samples were collected in October 2006 (spring). Sites were located in subtropical rainforest except for those at 1100 m which were in cool temperate rainforest where *Nothofagus moorei* (F. Muell) Krasser was dominant. Specimens collected were identified to species or morphospecies. Over 60 taxa (species and morphospecies) were identified from more than 7000 specimens. Species assemblages were significantly related to altitude generally showing a progressive change in composition with increasing altitude. Assemblages at the highest altitude of 1100 m were particularly distinct and several taxa were restricted to this altitude. Altitudinal patterns of assemblages of Collembola are compared with those of some other invertebrates from the same transect and suggestions for the differences offered. A review of altitudinal zonation in Collembola in various regions and climatic zones is provided. ❒ *Nothofagus, rainforest, montane faunas, altitudinal zonation, Paronellidae, Entomobryidae, Odontellidae, Symphypleona, Isotomidae, Hypogastruridae, IBISCA*

It is now generally accepted that global warming is accelerating and has the potential to alter considerably the distribution of both biological communities and their component species. If we are to conserve biological diversity and the ecosystem services it provides, we first need to document the possible effect of climate change on vulnerable faunal assemblages. This will not only improve understanding of the potential for natural processes of adaptation to occur (or not, as the case may be) but also to identify target organisms for monitoring such changes.

The IBISCA (Investigating the Biodiversity of Soil & Canopy Arthropods)-Queensland (Qld) project at Lamington National Park aimed to sample fauna and flora along a transect of increasing altitude to provide baseline data on species' distributions as temperature decreases and rainfall increases (Kitching *et al.* 2011). From this baseline information, we can recognise species or other taxa that have limited ranges along the transect. The overall aim of the project was to identify taxa that are 'climate responders' so that they can be monitored on a regular basis using focused sampling strategies. Any alterations in distribution of these taxa over time could be detected by monitoring, unless they are very rare. In an otherwise largely undisturbed environment the change may be assumed to be the result of climate variation, if the direction of the altered change is the same as that predicted to occur as a result of climate change. Of course, such monitoring needs to occur on a regular basis over a long enough time scale to overcome the impacts of short-term climatic variability. Data on indicator taxa could feed into management decisions in subtropical regions and become key components of monitoring/management systems. A considerable number of taxa have been surveyed within this project and Collembola (springtails) were one target group. Springtails are particularly suitable for including in such a study as they are abundant and species-rich in the Lamington National Park (Rodgers & Kitching 1998, 2010). Collembola can also be quickly and easily collected using a range of methods.

The collembolan fauna of subtropical forest is little known in Australia, or indeed anywhere in the world. To date, only ten named species of Collembola have been recorded in the published literature from Lamington National Park (Greenslade & Sutrisno 1994; Rodgers & Kitching 2010) and 24 species of Entomobryidae, mainly unidentified, were recorded from the canopy at 700 m above sea level (a.s.l.) in an unpublished thesis (Sutrisno 1994). The same is true of altitudinal zonation of collembolan faunas in general and only a few studies have been conducted of ground-living Collembola (Leakey & Proctor 1987; Bedos 1994; Gabriel *et al.* 2001; Greenslade 2004), none of these being in subtropical climes. Relevant data from these studies has been compared to the Lamington results reported here.

Here, the composition and other characteristics of the collembolan fauna at the different altitudes, sampled for the IBISCA-Qld project in pitfalls on a single occasion, are documented and the wider implications of these findings discussed in relation to species at risk of extinction under a hotter, drier climatic regime. Based on data from other invertebrate taxa, the hypotheses to be tested by the IBISCA-Qld project will be that different assemblages of species occur at different altitudes and that abundance and species richness diminishes as altitude increases.

MATERIALS AND METHODS

The trapping programme formed the basis of the IBISCA-Queensland project in the subtropical rainforest of Lamington National Park and used consistent and repeatable collecting methods in 20 plots at five altitudes; four replicates per altitude (see Kitching *et al.* 2011). The plots are permanently marked and cover altitudes from 300 to 1100 m a.s.l. at intervals of two hundred metres (Laidlaw *et al.* 2011). A brief description of the vegetation at each alititude is given in Table 1. Altogether, this project used seven baseline sampling methods in three major sampling events (October 2006, March 2007 and January 2008) (Kitching *et al.* 2011). All methods collected Collembola but only samples from pitfall traps set in October 2006 are reported here.

At each of the 20 plots, an array of nine pitfalls were set and left in the ground for nine days. They were arranged in a cross grid with each trap being a minimum of one metre from the nearest one. Traps were 50 mm in diameter (a 120 ml plastic vial within a PVC sleeve) with an aperture diameter of 43 mm and filled with 70% ethanol. Catches from the nine traps were combined before sorting. Collembola were identified to species or morphospecies and counted. All specimens have been deposited in

TABLE 1. Vegetation type and dominant plant species present for each altitude sampled along the transect in Lamington National Park. *From Sattler *et al.*, 1999.

Altitude (m a.s.l.)	Regional Ecosystem*	Description
300	12.8.4	Complex notophyll vine forest on Caenozoic igneous rocks with *Araucaria cunninghamii, Argyrodendron actinophyllum, Baloghia inophylla, Brachychiton acerifolius, Dendrocnide excelsa, Diospyros pentamera, Dysoxylum fraserianum, Toona ciliata* and *Orites excelsus.*
500	12.8.3	Complex notophyll vine forest on Caenozoic igneous rocks with *Argyrodendron trifoliolatum, Olea paniculata, Castanospermum australe, Cryptocarya obovata, Ficus macrophylla, Syzygium francisii, Diploglottis australis, Pseudoweinmannia lachnocarpa, Podocarpus elatus, Beilschmiedia obtusifolia, Neolitsea dealbata* and *Archontophoenix cunninghamiana.*
700 and 900	12.85	Complex notophyll vine forest on Caenozoic igneous rocks with *Argyrodendron actinophyllum, Cryptopcarya erythroxylon, Ficus watkinsiana, Dysoxylum fraserianum, Caldcluvia paniculosa, Geissois benthamii, Orites excelsus, Acmena ingens, Syzygium corynanthum, S. crebrinerve* and *Citronella moorei.*
1100	12.8.5	Simple microphyll fern forest on Caenozoic igneous rocks with *Nothofagus moorei* and/or *Doryphora sassafras, Caldcluvia paniculosa* and *Orites excelsus.*

the South Australian Museum and a voucher collection at the Arthropod Biodiversity Laboratory, Griffith University, Nathan. Some species have been bar-coded (Bar-coding of Life Project).

Average temperatures at the sites range from 18°C at 300 m a.s.l. to 15°C at 1100 m a.s.l. Average maxima and minima temperatures range from 28°C to 5°C, being highest at lowest altitudes. Total annual rainfall is around 1200 mm at 300 m a.s.l. and increases gradually with altitude to around 2400 mm at 1100 m a.s.l. (Australian Government, Bureau of Meteorology 2008). A set of environmental variables was assembled from data presented in other papers within this volume (Laidlaw *et al.* 2011; Strong *et al.* 2011). For each plot, this set included data on vegetation (basal area, number of stems, plant species richness), climate (minimum temperature, median temperature, maximum temperature and atmospheric moisture), soils (moisture, pH, organic content, NO_3, P, K, and Ca) and volume of decaying timber (standing and fallen).

Relationships between the composition of collembolan assemblages from each plot were examined using non-metric multidimensional scaling (NMDS) ordination using Bray-Curtis similarity values of species and morphospecies abundance (log transformed) data. PERMANOVA (permutational multivariate ANOVA, Anderson *et al.* 2008) was conducted to statistically investigate the effect of altitude on collembolan assemblage composition. PERMANOVA is analogous to traditional multivariate ANOVA, except that it calculates statistics (pseudo-*F* values) from distance measures of assemblage similarities between sites, and *P* values using permutational techniques (we used 999 permutations). Post-hoc pairwise comparisons were also conducted using 999 Monte-Carlo permutations between altitudes. Vectors of environmental variables were fitted onto the NMDS ordination. The direction of each vector represents the gradient of the environmental variable and its length is proportional to the correlation between the ordination and environmental variable. Only environmental variables with significant correlation coefficients (at a significance level of $P<0.05$ based on 999 random permutations) were overlaid on the ordination. Analyses were performed using PRIMER 6 (Clarke & Gorley 2006).

A similar transect across an altitudinal gradient was sampled for Collembola with pitfall traps in southern Tasmania (Grove *et al*. 2004; Greenslade 2004). Some data from this transect has been included for comparison with the Lamington data to compare latitudinal differences in zonation.

RESULTS

Over 60 collembolan taxa at the species and morphospecies levels were identified from more than 7000 specimens (Table 2). Species richness and abundance increased with altitude to 900 m but then fell at 1100 m (Table 3). However, the number of families trapped at each altitude did not differ markedly. The contribution that each family made to the total numbers of individuals trapped at different altitudes varied (Fig. 1, Table 4). The most abundant families trapped were the Paronellidae and Entomobryidae and the Paronellidae was more abundant at the lowest altitude. Families Odontellidae, Hypogastruridae and Dicyrtomidae were most abundant in traps at the highest altitude, and the Isotomidae and Neanuridae were most abundant at both 900 and 1100 m. Other families tended to be most abundant at 900 m, including the Entomobryidae, Katiannidae and Sminthuridae. Sminthurididae were not trapped above 700 m. Other families did not show a strong pattern of distribution or were present in insufficient numbers for the data to be meaningful.

The numerically dominant paronellid was *Pseudoparonella queenslandica* Schött, and in the Entomobryidae was *Acanthocyrtus spinosus* Schött, both fairly widespread species in eastern Australia and common along the entire altitudinal transect, although less abundant at 1100 m (Table 2). Other species showed some altitudinal restrictions (Table 2). *Epimetrura rostrata* Sutrisno and Greenslade (Entomobryidae) was found exclusively, but in small numbers, at 700 m. It has previously been shown to be abundant in the canopy at this altitude where it was found to comprise nearly 60% of total Collembola (Sutrisno 1994). Two species belonging to two different isotomid genera showed different and sequential preferences as regards altitude. A species belonging to the *Cryptopygus antarcticus* Willem group was found most abundantly at 1100 m and rarely at 900 m while a species of *Isotopenola* was found at 700 and 900 m only. The only tomocerid species, a member of the southern genus *Lepidophorella*, was found commonly along the transect but mainly at mid-altitudes. In the frequent but not abundant Symphypleona, a small number of specimens of a species of the rare genus *Adelphoderia* was found only at 500 m. Members of the leaf litter inhabiting Katianninae were more frequent and abundant at 900 m, while the epigaeic *Rastriopes* and *Sphyrotheca* in the Bourletiellidae were more abundant at the lower altitudes. Apart from a rare *Xenylla* species, the Hypogastruridae was represented only by a species of *Triacanthella*, not entirely restricted to but more frequent and abundant at 900 and 1100 m. It should be noted that as only pitfall collections are reported here, rare species in these collections could indicate that the species is not active on the ground surface but may be more common in a soil habitat for instance. The humidity-loving Odontellidae were represented by several species at high altitude and the single species of the Uchidanurinae (*Acanthanura* sp., Neanuridae), an endangered subfamily in Australia (Greenslade 1991a), was trapped only at 1100 m in the *Nothofagus* forest.

We identified five 'sentinel' species (Table 5), represented by multiple specimens collected from only a single elevation, that are promising candidates for future monitoring of climate change; *Pseudachorutinae* sp. 2 and *Acanthanura* sp. (both Neanuridae) restricted to 1100 m a.s.l., *Pseudachorutinae* sp. 1 (Neanuridae) only at 900 m, *Adelphoderia* sp. (Katiannidae) only at 500 m, *Rastriopes* sp. 2 (Bourletiellidae) only at 300 m.

The ordination grouped the plots at 1100 m into a tight and well-separated cluster but

TABLE 2. List of Collembola taxa collected in pitfall traps along the IBISCA-Qld transect and total numbers of individuals trapped at each altitude (summed across four replicate plots) with an estimate of preferred altitude for selected taxa (*300 m, **500 m, ***700 m, **** 900 m, *****1100 m) (brackets denote a weaker response at the altitude they enclose).

	300	500	700	900	1100	Preferred Altitude
ARTHROPLEONA (Poduromorpha)						
Neanuridae						
Acanthanura sp.	0	0	0	0	4	*****
Ceratrimeria sp.	1	0	2	23	0	****
Pseudachorutinae sp. 1	0	0	0	2	0	****
Pseudachorutinae sp. 2	0	0	0	0	6	*****
Pseudachorutinae sp. 3	2	1	1	0	12	*****
Neanurinae Lobellini	0	0	0	2	0	****
Paleonura sp.	0	0	0	0	2	*****
Odontellidae						
Indeterminate spp.	0	1	36	33	96	**(**)*
Brachystomellidae						
Brachystomella sp.	1	0	0	0	0	unclear
Hypogastruridae						
Triacanthella sp.	0	0	3	11	23	***(*)*
Xenylla sp.	2	0	0	2	0	unclear
ARTHROPLEONA						
Isotomidae						
cf. *Folsomina* sp.	0	0	0	0	2	*****
Cryptopygus antarcticus grp	0	0	0	2	14	***(*)*
Proisotoma sp.	0	0	0	0	1	unclear
Isotopenola sp.	0	0	8	12	0	**(*)*
cf. *Parisotoma*	0	0	0	2	2	****(*)
Isotoma tridentifera	12	0	4	32	5	widespread
Acanthomurus sp. 1	0	0	0	6	19	(*)****
Acanthomurus sp. 2	0	0	0	0	2	*****
Tomoceridae						
Lepidophorella sp.	0	13	30	20	5	*(*)**
Entomobryidae						
Lepidocyrtoides sp. 1	31	51	45	1	12	widespread
Lepidocyrtoides sp. 2	75	24	11	63	4	widespread
Epimetrura rostrata	0	0	0	20	0	****
?*Acanthocyrtus* sp. 1	151	64	90	208	1	absent 1100
Entomobryidae sp. 1	221	116	12	0	3	*(*)
Entomobrya sp. cf. *virgata*	1	0	8	3	2	widespread

TABLE 2. cont…

	300	500	700	900	1100	Preferred Altitude
Entomobrya varia	19	8	9	5	0	absent 1100
?*Sinella* sp.	1	1	7	12	11	unclear
Discocyrtus sp. cf. *cinctus*	0	1	59	213	71	****(*)
Lepidocyrtus sp. 1	4	126	47	90	0	absent 1100
Lepidocyrtus sp. 2	33	63	27	164	0	absent 1100
Lepidocyrtini sp. 3	13	38	65	14	6	widespread
Acanthocyrtus sp. 2	40	2	127	141	0	absent 1100
Indet. sp. 2	0	0	0	1	0	unclear
Immature Entomobryidae	216	133	338	208	22	
Paronellidae						
Pseudoparonella queenslandica	681	244	90	220	40	*
Paronellides sp.	0	0	0	5	0	****
Paronellidae sp. 1	19	29	55	68	48	widespread
Paronellidae sp. 2	5	58	39	42	30	widespread
Paronellidae sp. 3	0	55	24	12	9	widespread
Paronellidae sp. 4	0	1	1	2	0	widespread
Salina sp.	0	0	1	0	0	unclear
Immature Paronellidae	152	162	163	82	108	
SYMPHYPLEONA						
Immature Symphypleona	8	11	0	17	0	
Sminthurididae						
Sphaeridia sp.	5	0	6	0	0	widespread
Katiannidae						
Arrhopalites sp.	0	0	1	0	0	unclear
Adelphoderia sp.	0	3	0	0	0	**
Sminthurinus sp.	5	1	0	4	3	widespread
Sminthurinus sp.	0	1	0	0	2	unclear
Katianna sp. 1	0	2	1	138	33	****
Katianna sp. 2	0	1	4	0	10	widespread
Katianninae sp. 1	36	0	8	65	12	widespread
Katianninae sp. 2	0	1	0	1	4	*****
Immature Katiannidae	13	0	37	28	21	
Sminthuridae						
Temeritas sp. 1	1	0	29	3	2	***
Temeritas sp. 2	0	0	0	1	0	unclear
Sphyrotheca sp.	10	59	10	33	9	widespread

TABLE 2. cont…

	300	500	700	900	1100	Preferred Altitude
Pararrhopalites sp.	0	1	0	0	0	unclear
Bourletiellidae						
Bourletiellidae gen. indet. 1	2	0	0	1	2	widespread
Bourletiellidae gen. indet. 2	4	1	0	0	0	*
Rastriopes sp. 1	0	0	0	0	1	*
Rastriopes sp. 2	3	0	0	0	0	*
Dicyrtomidae						
Dicyrtomidae sp. 1	0	17	7	3	70	widespread
Dicyrtomidae sp. 2	0	1	0	23	0	****
cf.? *Calvatomina pagoda*	0	0	0	0	1	*****
Total Individuals	1767	1290	1405	2038	730	

TABLE 3. Numbers of species and individuals (abundance) of Collembola at each elevation along the IBISCA-Qld transect, Lamington National Park, and along transects at Warra (100–600 m a.s.l.) and Mt Weld (600–1300 m a.s.l.) in southern Tasmania.

	Elevation (a.s.l.) in metres												
Number of species	100	200	300	400	500	600	700	800	900	1000	1100	1200	1300
Lamington	-	-	31	-	33	-	34	-	44	-	40	-	-
Warra	22	21	17	23	20	15	-	-	-	-	-	-	-
Mt Weld	-	-	-	-	-	12	19	21	26	20	22	14	11
Abundance													
Lamington	-	-	1767	-	1290	-	1176	-	2038	-	730	-	-
Warra	329	299	277	302	148	121	-	-	-	-	-	-	-
Mt Weld	-	-	-	-	-	40	300	721	999	378	1522	532	520

the remainder of the plots showed less distinct groupings, in that assemblage composition tended to gradually change from low to high elevation (Fig. 2). PERMANOVA showed that altitude significantly influenced assemblage composition (pseudo-F = 4.34, $p<0.01$), with pairwise post-hoc comparisons showing significant differences between all pairs of altitudes except for 500 and 700 m and 700 and 900 m. The fitted vectors indicate the environmental factors that are significantly correlated with the ordination of collembolan assemblages (Fig. 2). Environmental factors positively correlated with the assemblages from higher altitudes were soil moisture, soil organic content, atmospheric moisture (all $p<0.01$) and soil nitrite concentration ($p<0.05$). Those correlated with assemblages from lower altitudes were tree species richness, high temperature, median temperature, higher soil pH, soil calcium levels, soil potassium (all $p<0.01$) and minimum temperature ($p<0.05$).

TABLE 4. Total abundance, individuals collected in pitfall traps, of each family of Collembola across the whole IBISCA-Qld transect and at each elevation at Lamington National Park.

Family	Altitude (m a.s.l.) 300	500	700	900	1100	Total
Neanuridae	3	1	3	27	24	58
Odontellidae	0	1	36	33	96	166
Brachystomellidae	1	0	0	0	0	1
Hypogastruridae	2	0	3	13	23	41
Isotomidae	12	0	12	54	45	123
Tomoceridae	0	13	30	20	5	68
Entomobryidae	805	627	845	1142	132	3551
Paronellidae	857	719	373	431	220	2600
Sminthurididae	5	9	6	0	0	20
Katiannidae	54	60	51	236	85	486
Sminthuridae	11	12	0	37	11	71
Bourletiellidae	17	18	7	18	3	63
Dicyrtomidae	0	18	7	26	71	122

DISCUSSION

Generalities suggested by the data presented here must be viewed with caution since they relate to one moment in time (October 2006) and are from pitfall catches only, so represent only the fauna active on the ground surface. Even so, they demonstrate some changes in collembolan assemblage composition with altitude. At the highest altitude (1100 m) showed a clear divergence in species composition compared with the other plots, there was a gradual trend along the altitude gradient of the collembolan assemblages towards 1100 m and few species were found at all altitudes. In addition, there was a change in family abundance with altitude. In support of these results, Maunsell (2009), comparing leaf litter faunas at the 700, 900 and 1100 m IBISCA-Qld plots, also found that the Collembola assemblage at 1100 m was distinctly different from the other two altitudes. Some altitudinal changes in numbers of individuals trapped, species richness and species distributions were also evident in this and Maunsell's (2009) study.

Of the few altitudinal studies that have been completed in Australia for Collembola, those at Warra and Mt Weld in Tasmania (Greenslade 2004) are the most relevant (Tables 3, 6, 7) and some altitudinal trends are also evident here. Lowest species richness and individuals trapped appeared to be at the mid-altitudes of 500 and 600 m (Table 3). This trend is not evident in the Lamington data. One similarity between the two latitudes is that of family distribution with the highest abundance of Isotomidae in traps in the Tasmanian study also being found at altitudes greater than 900 m (Table 7). Neanuridae and Odontellidae were also most abundant at high altitude in traps at 800 m, but not at 900 m probably because, unlike at Lamington, alpine vegetation, and not forest, was present at 900 m in Tasmania. However, differences in family distribution between the Queensland and Tasmanian sites are evident with Paronellidae being abundant at altitudes of 1200 and 1300 m on Mt Weld (Table 7) but being most abundant at the lowest altitudes (300 and 500 m) at Lamington. The effects of climate warming at the two latitudes are likely to lead to changes in family signatures at the different altitudes.

References to data from transects elsewhere are listed in Table 6. On two mountains in Tasmania and two in New Zealand, Andrew *et al.* (2003), using a flotation method of extraction from soil, found a decrease in invertebrate richness, including Collembola, with altitude and no change in abundance, these authors only identified invertebrates to family. In Sabah, Leakey and Proctor (1987) found a reduction in abundance of litter Collembola with increasing altitude but no change in soil Collembola, but these authors only used hand collections. Altitudinal studies from the Solomon Islands comparing coastal, forest and montane soil and leaf litter collembolan faunas found, as at Lamington and in Tasmania, a lower abundance

TABLE 5. List of Collembola 'climatic predictors', the elevation at which they currently occur and prediction of future changes under climate warming. * Only one specimen collected.

Species	Current distribution (m)	Possible change
Acanthanura sp.	1100	Local extinction
Pseudachorutinae sp. 1	900	Only at 1100 m
Pseudachorutinae sp. 2	1100	Local extinction
Odontellidae	500–1100	Eliminated from 500 m
Triacanthella sp.	700–1100	Eliminated from 700 m
Cryptopygus antarcticus grp	900–1100	Only at 1100 m
Isotopenola sp.	700–900	Eliminated from 700 m
Adelphoderia sp.	500	Local extinction
Rastriopes sp. 1	1100	Local extinction*
Rastriopes sp. 2	300	Elevation to 500 m
Sphyrotheca sp.	300–900	Extinction at 300 m

TABLE 6. Published data on species richness and abundance of Collembola with altitude.

Author/year sampled	Location	Altitudinal range (m a.s.l.)	Sampling method	Trends in abundance with increasing altitude	Trends in species richness with increasing altitude
This work/2006	Lamington NP, Queensland, Australia	300–1100	Pitfalls	Decrease at 1100m only	Increase
Greenslade/1965	Popamanusiu, Solomon Islands	ca.1000–1800	Tullgren funnel of leaf litter and soil	Decrease	Decrease
Bedos/1981–92	Don Inthanon, Thailand	>1000–2500	Tullgren funnel of leaf litter and soil	Rather higher	Rather higher
Leakey & Proctor/1983	Gunung Silam, Sabah, Malaysia	280-870	Hand sorting	Decrease in leaf litter fauna, no change in soil fauna	Not identified beyond Class
Andrew *et al.*/1996	Tasmania and New Zealand	250–1250 (Tas.) 650–2000 (NZ)	Flotation using kerosene	No change	Sometimes decrease in family richness but varied with mountain and country
Gabriel *et al.*/1996–99	Marion Island	50-1270	Tullgren funnel of soil	Not documented	Exotic species at lower elevation, native species at higher elevation
Greenslade/2001–2	Warra, Tasmania, Australia	100–600	Pitfalls and Malaise traps	Decrease	Decrease
Greenslade/2001–2	Mt Weld, Tasmania, Australia	600–1300	Pitfalls and Malaise traps	Decrease	Decrease

TABLE 7. Family signatures (numbers of individuals trapped in each family) for Collembola collected along altitudinal transects at Warra and Mt Weld, Tasmania.

Altitude (m a.s.l.)	Family											
	Bourletiellidae	Brachystomellidae	Dicyrtomidae	Entomobryidae	Isotomidae	Katiannidae	Neanuridae	Odontellidae	Paronellidae	Indet. poduromorphs	Indet. Symphypleona	Tomoceridae
Warra												
100 m	0	0	37	159	1	13	37	2	21	8	49	2
200 m	0	2	78	76	27	2	63	0	13	17	19	2
300 m	0	3	118	31	34	1	16	1	37	23	10	3
400 m	0	53	0	48	23	58	33	14	54	9	8	25
500 m	0	10	0	27	20	12	24	0	11	12	22	10
600 m	0	2	0	12	38	19	22	1	5	11	0	11
Mt Weld												
600 m	0	1	6	4	16	2	7	1	1	0	2	0
700 m	0	1	0	106	71	4	75	1	12	19	0	11
800 m	3	3	0	190	150	0	131	134	3	57	45	4
900 m	3	0	7	51	658	11	65	54	12	47	74	17
1000 m	9	1	9	37	153	6	35	0	46	11	61	10
1100 m	13	1	1	18	1324	2	3	0	16	5	137	2
1200 m	0	0	0	22	237	58	0	18	130	0	65	2
1300 m	0	0	0	10	326	16	3	56	109	0	0	0

of Collembola at montane sites (P. Greenslade unpub. data). The fauna at high altitude on Mount Popamanusiu in the Solomon Islands, at about 1800 m, lacked Symphypleona and Paronellidae and the proportion of Isotomidae and Tullbergiidae increased. No Tullbergiidae were found at Lamington or in Tasmania, but members of this family do not readily fall into pitfalls as they are soil-inhabiting. In fact, Isotomidae were best represented at the two highest altitudes both in the Solomons, at Lamington and in Tasmania.

The most comprehensive study of altitudinal zonation of Collembola was conducted in tropical rainforest on Doi Inthanon, Thailand (Bedos 1994). This author sampled soil and leaf litter at five altitudes over several years and recorded

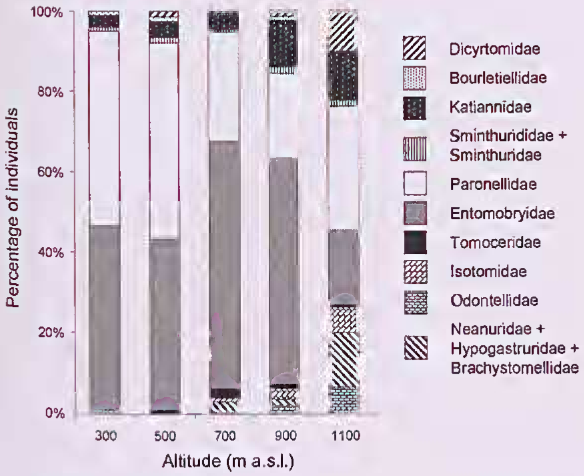

FIG. 1. Proportions of individual of collembolan families collected in pitfall traps at each of the five altitudes (summed across four replicate plots) along the IBISCA-Qld transect.

over 300 species in 106 genera of which only 13 genera also occurred at Lamington. As sampling methods were different, only a small overlap is expected. Most species (140) were collected at middle altitudes (1700–2100 m); the highest altitudes (2400–2550 m), where most samples were taken, had a slightly lower number of species (120) and the lowest altitudes least (109). As sampling was not standardised at all sites some bias in the data may have occurred. Abundance in terms of average individuals per sample was least (89) at intermediate elevations, highest (130) at the highest elevations and intermediate at the lowest elevations (Bedos 1994). Ordination showed some degree of separation with lower elevations (700–1150 m) clustering separately from higher elevations (1700, 2400 and 2550 m).

In a different climatic region on subantarctic Marion Island, species richness and abundance of springtails, collected by funnel extraction, were

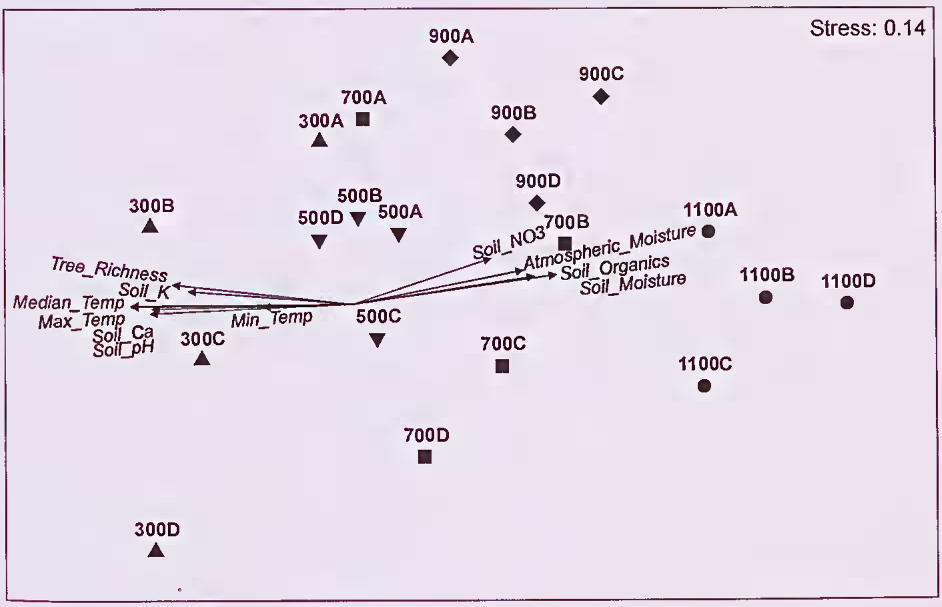

FIG. 2. Non-metric multidimentional scaling (NMDS) ordination plot of collembolan assemblages, based on log transformed abundances of species and morphospecies collected in pitfall traps along the IBISCA-Qld transect in October 2006. Superimposed vectors are environmental parameters significantly correlated ($P<0.05$) to the assemblage composition. ▲, 300 m a.s.l.; ▼ 500 m; ■ 700 m; ◆ 900 m; ●; 1100 m. A, B, C and D correspond to the replicate plots at each altitude.

analysed based on vegetation type (Gabriel *et al.* 2001). Species richness was highest in both the lowland tussock grassland and high altitude fell field sites (9 spp) and lowest in the high altitude mire (5 spp), while mean annual density of all species varied from 305 individuals per m^2 in the mid-altitude fell field to 60733 individuals per m^2 in the *Cotula plumosa* community (Gabriel *et al.* 2001).

In summary there appear to be a few generalisations that can be made concerning changes in diversity and abundance of Collembola with altitude. At most localities, abundance and species richness are lower at the highest altitudes than at mid- or sub-summit altitudes. This agrees with the conclusions of Zapata *et al.* (2003) who tested the null hypothesis that altitudinal or latitudinal gradients exhibit a mid-gradient peak in species richness and concluded that it was not supported. Another common factor is that at Lamington, Tasmania and the Solomon Islands, hemiedaphic and euedaphic families, Isotomidae (and Tullbergiidae in the Solomons), are more abundant at the summit, regardless of actual altitude, while Symphypleona, Entomobryidae and Paronellidae, more epigaeic groups, are in low abundance here or even absent altogether. This is a characteristic that can be demonstrated more widely if one assumes that high altitudes and high latitudes present similar environmental features. For instance, at extremes of latitude, Antarctic faunas lack Symphypleona, Entomobryidae and Paronellidae (Gabriel *et al.* 2001). From this and the Tasmanian data, biotic factors, in particular vegetation structure such as the presence or absence of forest cover, appear to influence the occurrence of families at different localities more than altitude or climate *per se* which exert only an indirect effect through their effects on vegetation. One other possible generalisation is that where species data exist, it appears that a different suite of species, but not genera or families, occurs at the summit of all mountains sampled regardless of location, vegetation and altitude (Greenslade 2008).

The results for Collembola from the Lamington transect that showed only the plots at 1100 m had a distinctly different composition are similar to assemblage patterns of some other invertebrate groups sampled from the same plots. An exception was the ants which showed a linear response to altitude with species richness progressively decreasing and assemblage composition progressively changing with increasing altitude (Burwell & Nakamura 2011). This is probably a response to decreasing temperatures and increasing soil moisture (Strong *et al.* 2011). The data for Coleoptera, some Hemiptera and macrolepidoptera also indicated that the most distinct species assemblages occurred at 1100 m (Ashton *et al.* 2011; Ødegaard & Diserud 2011), although this separation seems most marked for Collembola.

One reason for this may be that ground-living, (that is soil and leaf litter) organisms are less responsive to slight shifts in climatic variables compared with epigaeic species that live predominately above the ground and Collembola are the only ground-living decomposer guild that has been analysed from these studies to date. Collembola may be more strongly influenced by the depth and moisture content of the leaf litter and humus layers than the other invertebrates studied. The pH of the soil becomes more acidic with increasing altitude along the IBISCA-Qld gradient (Laidlaw *et al.* 2011; Strong *et al.* 2011) and Loranger *et al.* (2001) suggested that soil acidity is the primary factor influencing altitudinal distribution of Collembola. It is noteworthy that the vegetation at the highest altitude, 1100 m, is the only site where relictual Gondwanan *Nothofagus* rainforest occurs. We suggest that the main reason for the distinctiveness of the fauna here is that it is largely composed of relictual invertebrate species from Gondwana while lower altitudes tend to harbour more recent and widespread lowland taxa.

A number of species, mainly from the Entomobryidae and Paronellidae, are widespread along the transect. Their value as 'climate responders' is minimal. However several potential climate responders, that is taxa that appear to have limited altitudinal distributions, were detected in other families, based on the results of a single trapping period and single method (Table 5). First are those, *Rastriopes* sp. and *Spyrotheca* sp., that were found mainly (80%) at the lowest altitudes. *Rastriopes* belonged to the Bourletiellidae, an epigaeic family most abundant and diverse in warm climates and in summer (Greenslade 1991b). It might be expected that under climate change, their altitudinal range would increase. Of most importance are the two species, *Acanthanura* sp. and a species of Pseudachorutinae, only found at 1100 m. In spite of low numbers trapped, we consider that they are truly altitudinally restricted species based on the biology of allied species. Also important is a new species of *Adelphoderia*. This genus is found only where water logging occurs sporadically (Greenslade 1982). It was trapped at a single IBISCA-Qld 500 m plot in close proximity to a creek. Only the 500 m (and some 300 m) sites were close to permanent creeks (there being no other accessible 'drier' sites available at those altitudes). This may well be the explanation for why this species was restricted to the 500 m plot, yet it may well occur at other altitudes close to creek lines. The Odontellidae were not identified to species but about five species were present. It is possible that some might be even more restricted than the family as a whole. They would repay further study. The genus *Triacanthella* has an unusual distribution in Australia being found not only in montane situations as in this study and elsewhere but also sometimes in semiarid mallee or *Melaleuca* and *Casuarina* woodland in coastal situations. It is also found in boreal regions but has not been recorded in the tropics. Finally results for the two genera with sequential distributions, *Cryptopygus* (found at 900-1100 m) and *Isotopenola* (700-900 m) reflect their wider distribution in the Southern Hemisphere. The genus *Cryptopygus* occurs in the Antarctic, subantarctic and southeastern Australia but only in cool, moist localities. On the other hand, *Isotopenola* is not found in the Antarctic or subantarctic but is fairly common in humid parts of south eastern Australia and is found in a wider range of climatic conditions than *Cryptopygus*, indicating that it is tolerant of somewhat warmer conditions. The relative distributions of the species in these two genera clearly suggest they are also candidates as 'climatic responders'.

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